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Invasive birds in a novel landscape: habitat associations and effects on established species

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Studying the relationships among introduced species, their preferred habitats, and native species can be important for predicting the effects of invasions on native populations. Examining the colonization of North America by the Eurasian collared-dove *Streptopelia decaocto*, we quantified the habitat characteristics of sites most likely to be occupied by this invasive bird species in the early stages of the invasion. Further, we studied the relationship between collared-dove abundance and the abundance of other dove species in the study area, anticipating a negative effect on established species following the introduction of a potential competitor. Linking satellite-derived landcover data with winter bird community data gathered from 444 study sites in Florida, USA from 1999 to 2008, we found that collared-doves were more likely to occur in landscapes that had been highly-modified by human activity than in forested landscapes. Collared-dove abundance increased as the proportion of the landscape characterized as low-intensity development and medium/high-intensity development increased. The probability of collared-doves occurring at a site was also related to the spatial proximity of other sites reporting doves (positive spatial autocorrelation). Contrary to our expectations, the site-level abundance of four other dove species all increased with collared-dove abundance throughout the sampling period. Interactions between collared-doves and native species should be further studied in different environments as this invasive bird rapidly colonizes North America.

Although biological introductions and invasions are considered to be among the top five drivers altering global biodiversity (Sala et al. 2000), the potential ecological impacts of introduced species on native communities are vast and remain largely undocumented (Duncan et al. 2003, Gurevitch and Padilla 2004, Didham et al. 2005). Understanding the patterns of colonization and persistence of invasive species is critical for mitigating potentially negative interactions between exotic and native species. We face major challenges, however, in detecting and monitoring populations of invasive organisms at relevant spatial and temporal scales across a full range of land cover contexts. Long-term bird-monitoring programs provide data at the temporal and spatial scales large enough to adequately track the spread of invasive birds, allowing us to investigate the characteristics of sites that are initially colonized as a species becomes established in a novel area, and to quantify the impact of the invasive species on populations of ecologically similar natives.

Using a combination of bird monitoring data and satellite-derived land cover information, ecologists have made great progress in modeling relationships between habitat variables and bird distribution or abundance (Venier et al. 2004, Gottschalk et al. 2005). Such efforts have increased our ability to identify key characteristics of sites likely to be occupied and to further predict the distribution of a species across a landscape (Kerr and Ostrovsky 2003, Bustamante and Seoane 2004). Once established, rapidly expanding populations of non-native species can negatively affect native species through competitive exclusion, niche displacement, predation, or other interactions (Mooney and Cleland 2001). Quantifying the landscape-scale characteristics favored by invasive species can be particularly important in attempting to predict the effects of invasives on native populations (Eraud et al. 2007) and identify areas that have a high probability of future colonization.

Historic colonization events have altered avian communities at local and continental scales (Wootton 1987, Strubbe and Matthysen 2007). For instance, the non-native European starling *Sturnus vulgarus* and house sparrow *Passer domesticus* may compete for nesting sites with native cavity-nesting birds in North America (Ingold 1998). Because both of these species were introduced and established during the 19th century, however, the patterns and processes of their initial colonization are poorly understood and the influence of exotic birds on native avian communities remains a subject of debate (Koenig 2003).

A contemporary colonization event presents an opportunity to study the invasion of North America by a rapidly expanding non-native species, allowing for close

examination of colonization patterns (Hengeveld 1993). The Eurasian collared-dove *Streptopelia decaocto*, hereafter "collared-dove" was first established in continental North America in the state of Florida, USA, in the early 1980s and has rapidly spread (Smith 1987, Romagosa and Labisky 2000). Competitive interactions between collared-doves and native doves have not been adequately explored, but the potential for negative interactions exists (Romagosa and Labisky 2000, Hayslette 2006).

Here we combine land cover data and standardized bird observations to identify landscapes initially colonized by the collared-dove. Our first objective is to identify the landscape-scale characteristics that best predict the occurrence of collared-doves in Florida. We test a suite of models designed to identify the land cover compositions and configurations most widely used by the collared-doves. Second, we examine the relationship between collared-doves and other Columbidae during winter, exploring the potential for competitive interactions between collared-doves, mourning doves *Zenaida macroura*, white-winged doves *Z. asiatica*, common ground-doves *Columbina passerina*, and rock pigeons *Columba livia*. The invasive collared-doves are associated with human development throughout Europe and Asia (Coombs et al. 1981), so we predicted that collared-doves would be more likely to occur in human-dominated landscapes in Florida. Further, observations suggest that the collared-doves may be aggressive and behaviorally dominant over similar species (Romagosa and Labisky 2000), so we predicted that the abundance of ecologically similar species would be inversely related to collared-dove abundance.

Methods

Data on dove populations were collected by Project FeederWatch (PFW), a citizen science program operated by the Cornell Lab of Ornithology and Bird Studies Canada. Wells et al. (1998) report full details of the PFW protocol. In brief, program participants record the maximum number of each species seen from a single location near a supplemental feeding station during periodic, repeated, two-day counts. More than 10 000 PFW sites are located across the United States and Canada annually, with as many as 22 counts submitted from each site between November of one calendar year and April of the next calendar year. We have limited our analyses to 444 sites located in Florida and monitored between November 1999 and April 2008 ($n = 10\,335$ counts, Fig. 1). We focused on counts conducted in these years because the project did not consistently collect data on collared-doves before this period. The timing of counts is standardized and no trends exist in the timing of counts among seasons (which could bias results if a temporal trend in the timing of counts existed).

Landscape analysis

Using a 1 km buffer around each PFW site, we analyzed the 2001 National Land Cover Data (NLCD) to characterize the composition and configuration of different land cover

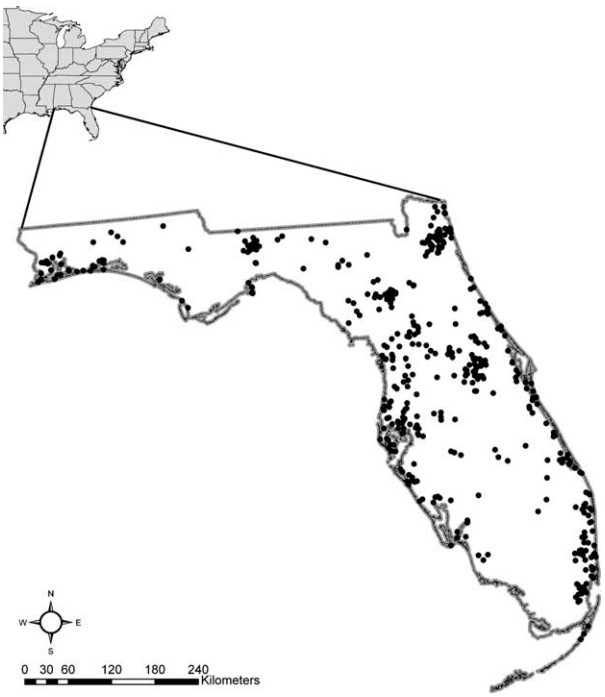

Figure 1. Distribution of Project FeederWatch sites surveyed between 2000 and 2008 in Florida.

types in the surrounding landscape. The 2001 NLCD consists of 16 land cover classes modeled over the conterminous United States at a 30 m cell resolution and a 0.40 ha minimum mapping unit (Homer et al. 2007). We aggregated the land cover classes to represent 5 major land cover types including agriculture (cultivated, pastures, orchards, and herbaceous), forest (deciduous, evergreen, and mixed forest types), open (lawns and suburban grasslands with impervious surfaces accounting for $<20\%$ of total cover), low-intensity developed (impervious surfaces account for 20–49% of total cover), and medium/high-intensity developed (impervious surfaces account for 50–100% of total cover). For each landscape, we calculated a suite of class-level metrics describing the landscape context of each site including the proportions of forest (FOR), low-intensity development (LDEV), medium- and high-intensity development (DEV), agriculture (AG), and open urban grasses (OPEN). We also calculated two configuration metrics including the number of forest patches (FORNP) and the number of patches of low-intensity developed land (LDEVNP). All landscape metrics were calculated using FragStatsBatch (Mitchell 2005) and FRAGSTATS (McGarigal et al. 2002). In addition to these land cover variables, we included information on the number of two-day count periods for each site between 2000 and 2008 (COUNT) as a measure of observer effort. We also calculated an autocovariate weighting (AUTO) for every site based on the proximity of sites with a positive occurrence of collared-doves between 2000 and 2008 (Augustin et al. 1996). The autocovariate is an index of demographic isolation that assigns weights to sites using the inverse linear distance such that higher weights are given to sites that are in closer proximity to other occupied sites. For the land cover analyses, sites were considered occupied

if a collared-dove was detected at the site at least once during a sampling season.

We used a logistic mixed model (form of the general linear mixed model; Pinheiro and Bates 2000, Faraway 2006) with AIC-based model selection (Anderson 2008) to identify the most parsimonious model of the relationship between landscape characteristics and the occurrence of collared-doves across PFW sites in Florida. We chose to use maximum likelihood (ML) estimates of fixed effects instead of the restricted maximum likelihood (REML). Although REML is an alternative to ML when the sole focus is estimation of unbiased variance components when dealing with small sample sizes, the likelihoods obtained for different models of fixed effects are not valid when comparing models using AIC (Pinheiro and Bates 2000). In this study, small sample size was not an issue and ML estimation was preferred in terms of model selection. To test our hypotheses concerning the relationship between collared-dove occurrence and landscape characteristics, we constructed an a priori set of 26 candidate approximating models with various combinations of land cover types, which represented a suite of ecologically plausible hypotheses (Burnham and Anderson 2002, Anderson 2008). To avoid the unit-sum constraint of using landscape composition metrics (Aebischer et al. 1993), we never included all land cover variables in a single model and all land cover metrics were tested for multicollinearity. We then ran all 26 land cover models with the additional autocovariate term resulting in a total of 52 models. The PFW site was included as a random factor to account for repeated surveys at individual sites across years. We calculated the log likelihood value, number of model parameters (K), AIC_C values, ΔAIC_C, and model probabilities (Prob(H|data)) following Anderson (2008). We calculated the area under the curve (AUC) as a measure of discriminatory power (Fielding and Bell 1997, Freeman and Moisen 2008). The AUC statistic represents the probability that a model will rank a randomly chosen positive occurrence higher than a randomly chosen negative occurrence. The use of AUC as a measure of predictive performance has been recently criticized, particularly in its application to species distribution modeling (Lobo et al. 2008). Two key criticisms are that AUC weights omission and commission errors equally, and that, with respect to distribution modeling, AUC scores are sensitive to the geographic extent of the study region. That is, including more sites that are beyond the environmental domain of a species will lead to higher AUC scores because those absences will tend to be well predicted. In our study, however, we are not comparing models between species and all models are based on precisely the same sets of data within the same geographic region. As a consequence, we believe that AUC, in combination with Nagelkerke R^2 values (Nagelkerke 1991), provides a reasonable measure of model discrimination.

Community analysis

For the community analyses, we focused on the relationship between the relative abundances of collared-doves and four ecologically similar species: mourning dove, white-winged dove, common ground-dove, and rock pigeon. Maximum counts from PFW are correlated with the abundance of a species in the local area (Wells et al. 1998, LePage and Francis 2002). For these analyses, the counts of each dove species recorded during a count period was $\ln(N+0.1)$ transformed, which effectively produced residuals with normal distributions. We chose the log-normal transformation because model diagnostics indicated overdispersion of the data, rendering the Poisson distributed error model inappropriate. We used linear mixed models in combination with model selection to model the relationships between the abundance of collared-doves and the abundance of the other dove species. Such an analysis, however, may be confounded by differences in habitat preferences among species (Cruz et al. 2006). Thus, we developed separate sets of candidate approximating models for each dove species using the same combination of land cover characteristics as those used for testing the distribution of collared-doves. In addition to these land cover variables, we added a second set of models that included the abundance of collared-doves during the count (LnCD). This approach allowed us to test the influence of collared-dove abundance on other dove species while accounting for habitat associations. For each count, PFW participants report the number of half-days on which observations were made over the 2-d count period and the total number of hours spent watching their feeders during the count period. All models included the number of half-days (NDAYS) and the number of effort hours (HOURS) to account for variation in observer effort. Year of sampling (YEAR) was also included to test for temporal trends in abundance. In all community models the PFW site was included as a random factor to account for site-based differences and because observations at sites were of a repeated measures design.

Models with normalized AIC_c weights which differed by <2 were deemed to be equivalent (Burnham and Anderson 2002). When several models had strong support as identified through model selection, we used model averaging to calculate weighted parameter estimates, unconditional standard error estimates, and unconditional confidence intervals (Anderson 2008). As a measure of model performance, we used the method outlined by Nagelkerke (1991) for a likelihood based analysis and report the Nagelkerke R^2 value for the best model. We used the lme4 package in R (R Development Core Team 2008) for all tests.

Results

Landscape analysis

The landscapes surrounding PFW sites were characterized by a diversity of land cover types and composition including AG ($\bar{x} = 8.4\%, 0–82.6\%$), OPEN ($\bar{x} = 30.4\%, 0–81.0\%$), FOR ($\bar{x} = 13.0\%, 0–77.5\%$), LDEV ($\bar{x} = 23.0\%, 0–87.1\%$), and DEV ($\bar{x} = 8.7\%, 0–79.3\%$). We found that the occurrence of collared-doves across Florida was influenced by the composition of land cover, survey effort, and proximity to other colonized sites. The model with the greatest support (Prob[H|Data] = 1.0) included the land cover variables of AG, OPEN, LDEV, LDEVNP, and DEV (Fig. 2). Most notably, the probability of

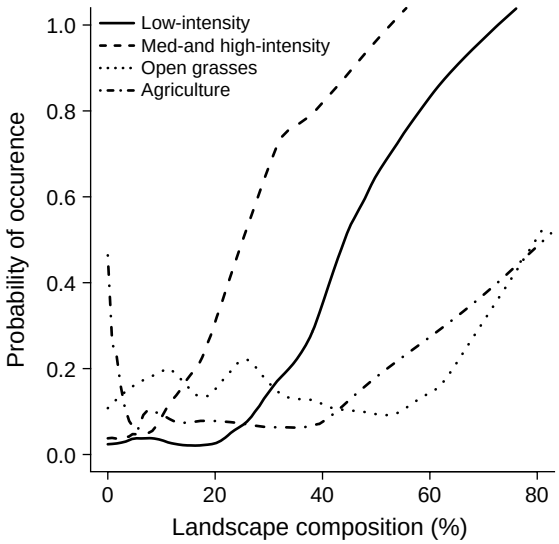

Figure 2. Estimates of the fixed-effects parameters from the fitted mixed model showing the predicted occurrence of collared-doves and important land cover types as identified through model selection. The probability of the occurrence of collared-doves demonstrated strong relationships with human-modified land cover types such as low-intensity and medium/high-intensity development. We found weaker relationships with agricultural and open cover types. Lines were generated using a locally weighted (LOWESS) smoothing curve.

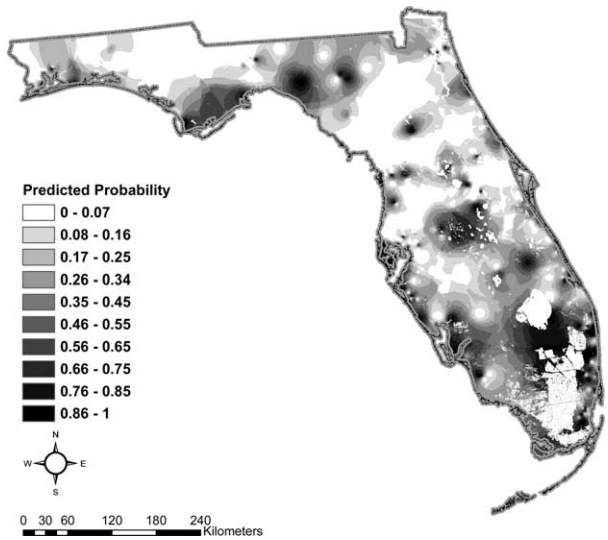

Figure 3. An interpolation of the predicted probability of occurrence of collared-doves generated from the best model in our landcover analysis. Predicted probabilities for each site were interpolated using inverse-distance weighting (minimum neighborhood radius = 6 sites) and a 1 km resolution. Predictions were restricted to upland cover types. Dark areas represent areas with a high probability of occurrence and light areas have a low probability of occurrence.

occurrence of collared-doves increased when larger proportions of the landscape were classified as low-intensity development ($\beta_{LDEV} = 0.13$, SE = 0.036, Fig. 2) and medium/high-intensity development ($\beta_{DEV} = 0.17$, SE = 0.053). Further, collared-doves were associated with large contiguous blocks of development (i.e. negatively associated with fragmentation of developed areas, $\beta_{LDEVNP} = -0.21$, SE = 0.072). We also found weak, but positive associations of collared-dove abundance with agricultural ($\beta_{AG} = 0.076$, SE = 0.045) and urban open cover types ($\beta_{OPEN} = 0.11$, SE = 0.043). Additional land cover variables such as forest and forest configuration were not identified as being important predictors of collared-dove presence.

The presence of collared-doves was strongly affected by demographic isolation, where sites in closer proximity to other occupied sites were more likely to be occupied ($\beta_{AUTO} = 16.48$, SE = 4.12). The probability of detecting collared-doves also increased with greater survey effort ($\beta_{COUNT} = 0.26$, SE = 0.05). The top model had adequate discriminatory power (AUC = 0.75), and a Nagelkerke R^2 value of 0.28. The predicted probabilities interpolated from the top model, described above, are useful for visualizing hot spots of occurrence (Fig. 3). We found that the highest probabilities of occurrence were concentrated in the southeastern section of Florida, the initial site of invasion of collared-doves in North America.

Community analysis

Of the 444 sites included in this analysis, collared-doves were detected at 143 sites, mourning doves at 417 sites, common ground-doves at 121 sites, rock pigeons at 80 sites, and white-winged doves at 100 sites. Contrary to our predictions, the abundance of other dove species was positively correlated with the abundance of collared-doves (Fig. 4). For mourning doves, four top models ($\Delta AIC_c < 2$) had varying amounts of support, given the data (Table 1). Models that did not include the abundance of collared-doves at a site were not supported. Rather, the inclusion of collared-dove abundance as a covariate in the top four models had strong cumulative support (Prob(H|data) = 0.78). Model averaging across these four models found that mourning doves were more abundant at sites with more collared-doves ($\beta_{LnCD} = 0.10$, SE = 10.016, 95% CI = 0.06–0.13). Mourning dove counts declined slightly over the survey period (2000–2008, $\beta_{YEAR} = -0.027$, SE = 0.004, 95% CI = −0.03–−0.020). In terms of land cover characteristics, the percentage of the landscape that was agricultural (AG) and open (OPEN) was included as a covariate in all four top models, and mourning doves were generally less abundant in agricultural ($\beta_{AG} = -0.009$, SE = 0.003, 95% CI = −0.016–−0.004) and open landscapes ($\beta_{OPEN} = -0.004$, SE = 0.002, 95% CI = −0.009–0.001). Mourning doves were more abundant in residential landscapes and less abundant in highly developed areas. Increased observer effort led to higher reported abundances. The top model explained a relatively large amount of variation in mourning dove abundance across sites (Nagelkerke $R^2 = 0.58$).

For common ground-doves, four top models ($\Delta AIC_c < 2$) had varying levels of support (Table 1), and the global model did not explain as much variation (Nagelkerke $R^2 = 0.11$) as the mourning dove model. In addition to the year and effort covariates, the model with the greatest support (Prob[H|Data] = 0.26) included variables for LnCD, LDEV, LDEVNP, FOR, and FORNP. The second

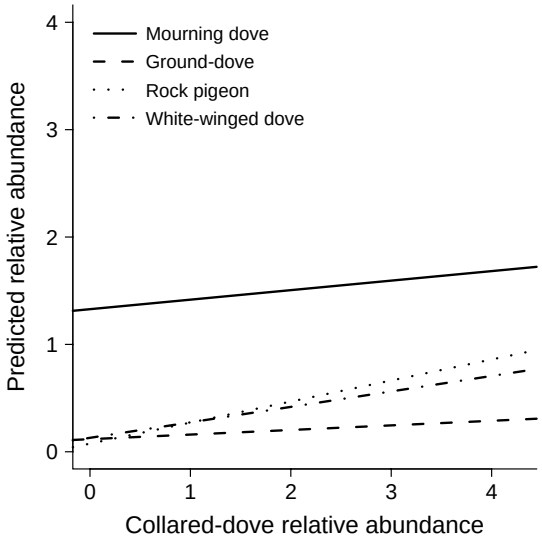

Figure 4. We found positive correlations between the abundance of collared-doves within a site and the abundance of other dove species including mourning doves, common ground-doves, rock pigeons, and white-winged doves. Axes are ln(N + 0.1) transformed values.

model ($\Delta AIC_c = 0.9$, Prob[H|Data] = 0.12) did not include LnCD but did include LDEV, LDEVNP, FOR, and FORNP. Model averaging across these four models demonstrated a weakly positive correlation between common ground-dove abundance and the abundance of collared-doves, however the unconditional 95% confidence interval included zero ($\beta_{LnCD} = 0.012$, SE = 0.009, 95% CI = −0.006–0.03). Similar to the mourning doves, counts of common ground-doves declined over time, although the unconditional confidence interval included zero ($\beta_{YEAR} = -0.003$, SE = 0.002, 95% CI = −0.006–0.000). Landscape characteristics were important in all top competing models, and common ground doves were less abundant at sites with greater amounts of low-intensity development ($\beta_{LDEV} = -0.001$, SE = 0.001, 95% CI = −0.003–0.002) and forest cover ($\beta_{FOR} = -0.002$, SE = 0.001, 95% CI = −0.005–0.000).

We found similar patterns for rock pigeons and white-winged doves, although these species were less ubiquitous. For rock pigeons, the models with strongest support (Prob[H|Data] = 0.78) included the variables LnCD, AG, OPEN, LDEV, DEV, and LDEVNP (Table 1). We found that rock pigeons were positively associated with the abundance of collared-doves ($\beta_{LnCD} = 0.051$, SE = 0.008, 95% CI = 0.04–0.07), but were declining throughout the study period ($\beta_{YEAR} = -0.023$, SE = 0.002, 95% CI = −0.03– −0.02, Nagelkerke $R^2 = 0.40$). Rock pigeons were also more common in developed ($\beta_{DEV} = 0.013$, SE = 0.003, 95% CI = 0.008–0.02) and open urban landscapes ($\beta_{OPEN} = 0.004$, SE = 0.002, 95% CI = 0.000–0.008). With white-winged doves, the two top models (Prob[H|Data] = 0.65) also showed a positive correlation with collared-dove abundance ($\beta_{LnCD} = 0.069$, SE = 0.009, 95% CI = 0.05–0.09). Unlike the other dove species, white-winged doves increased in abundance over time ($\beta_{YEAR} = 0.030$, SE = 0.002, 95% CI = 0.026–0.034). In addition, white-winged doves were more abundant in landscapes characterized by higher amounts of agriculture ($\beta_{AG} = 0.006$, SE = 0.002, 95% CI = 0.001–0.01) and low-intensity development ($\beta_{LDEV} = 0.007$, SE = 0.003, 95% CI = 0.002–0.01). White-winged doves were negatively associated with forest cover ($\beta_{FOR} = -0.003$, SE = 0.003, 95% CI = −0.008–0.002) and were more common in areas with fewer forest patches ($\beta_{FORNP} = -0.002$, SE = 0.002, 95% CI = −0.005–0.01). The top model for white-winged doves explained a relatively high amount of variation (Nagelkerke $R^2 = 0.60$).

Discussion

Landscape analysis

Studies of invasion dynamics typically lack information on the relationship between landscape characteristics and the likelihood of successful colonization by a non-native species (With 2002). Our results indicate that collared-doves are more likely to occupy landscapes that have been highly modified by human activity than less disturbed landscapes. We found that collared-doves preferentially occupied suburban and developed landscapes in Florida (Fig. 2 and 3). In addition, collared-doves were more likely to occur in areas where development was less fragmented (i.e. landscapes dominated by large, aggregated blocks of development). In Spain, where collared-doves have also become established in recent years, researchers similarly discovered that the species initially colonized developed areas from which they later expanded into the surrounding rural landscape (Rocha-Camarero and DeTrucios 2002). Collared-doves in Britain are "invariably" associated with human settlements (both urban and rural) where grain is available (Coombs et al. 1981). The availability of grain may be a factor in Florida as well. Although suburban development was the strongest predictor of collared-dove occurrence, we also found a positive association with agricultural areas.

Species that are adapted for living in close association with humans often have increased potential for successful establishment in novel areas (Smallwood 1994, Allen 2006). Indeed, successful avian invaders in North America are generally well-adapted to thrive in highly modified landscapes (i.e. rock pigeon, European starling, house sparrow). Further, urban bird communities are typically dominated by granivores and sedentary or partially migratory species like collared-doves (Chamberlain et al. 2009).

There is an increasing recognition that urbanization facilitates colonization by invasive species (McKinney 2002, Chace and Walsh 2006, Blair and Johnson 2008, Hepinstall et al. 2008). One possible explanation for the increased prevalence of invasive species in urban environments is increased resource availability. Research suggests that the successful colonization of highly modified landscapes in Belgium by the invasive ring-necked parakeet *Psittacula krameri* is related to greater food supplies in developed areas (Strubbe and Matthysen 2007). Our study sites were located near supplemental feeding stations throughout a range of cover types and urbanization. As such, food was not limited at any site in our study regardless of landscape context, suggesting that the collared-doves were selecting

Table 1. Model selection table for the community analyses showing the top competing (ΔAICc <2.0) models for mourning doves (MODO), common ground-doves (COGD), rock pigeons (ROPI), and white-winged doves (WWDO). In addition to the variables listed below, all candidate approximating models included fixed effects for effort and the year of sampling. Site identifier was included in all models as a random effect. We report the number of model parameters (K), second-order bias corrected AIC (AICc), the difference in AICc values from the best model (ΔAICc), and model probabilities (Prob(H|data)).

Species	Top models and variables[a]								K[b]	AICc	Δ AICc	Prob(H|data)
	LnCD	AG	OPEN	LDEV	DEV	FOR	LDEVNP	FORNP				
MODO	X	X	X	X					14	18656.4	0.0	0.337
	X	X	X						13	18657.8	1.4	0.168
	X	X	X	X			X		15	18658.0	1.5	0.156
	X	X	X	X	X				15	18658.5	2.0	0.119
COGD	X			X		X	X	X	15	3702.9	0.0	0.256
				X		X	X	X	14	3704.4	1.5	0.121
	X			X		X	X		14	3704.4	1.5	0.120
	X		X	X		X	X	X	16	3705.0	2.0	0.088
ROPI	X	X	X	X	X				15	3830.3	0.0	0.282
	X		X	X	X				14	3830.4	0.1	0.268
	X		X	X	X		X		15	3832.1	1.8	0.115
	X	X	X	X	X		X		16	3832.1	1.9	0.110
WWDO	X	X	X	X	X	X		X	17	6436.3	0.0	0.426
	X	X	X	X					14	6437.6	1.3	0.227

[a]LnCd = Ln transformed collared-dove abundance, AG = agriculture (% of 1 km radius landscape), OPEN = urban grasses (%), LDEV = low-intensity development (%), DEV = medium- and high-intensity development (%), FOR = forest (%), LDEVNP = number of patches of low-intensity development, FORNP = number of forest patches.
[b]Number of parameters include number of survey hours (4 factor levels) and number of survey half-days (4 factor levels).

sites based on habitat and landscape preferences rather than on food availability per se.

In addition to land cover composition and configuration, we also found that collared-doves were more likely to occur at sites that were in close spatial proximity to other occupied sites – a similar pattern was found during the collared-dove invasion of Europe in the 20th century (Hengeveld 1988). Although we did not have the necessary data for documenting parameters such as dispersal distance and reproductive success, demographic isolation and spatial autocorrelation are generally considered key components of metapopulation dynamics (Koenig 1999). Recoveries of ringed collared-doves in Europe indicate that most birds disperse <250 km, although distances of up to 600 km have been recorded (van den Bosch et al. 1992).

Effect of invasion on other Columbids

Interactions between native and introduced organisms have been widely documented and may have significant implications for native species (Mooney and Cleland 2001). Although invasive species may be one of the leading causes of extinction (Wilcove et al. 1998, Clavero and Garcia-Berthou 2005), such drastic effects generally only result when the invader is at a higher trophic level than the affected natives (e.g. when novel predators are introduced on islands) or when invasives introduce novel diseases. Negative effects resulting from exploitative or interference competition for resources with introduced species at the same trophic level are far more difficult to document and quantify. In birds, it has been hypothesized that competition for nesting cavities between the introduced European starling and native cavity-nesting birds in North America has negatively influenced reproductive success in a variety of native woodpeckers (Ingold 1998). A continent-wide study of population trends in native cavity-nesting species, however, failed to detect a relationship between starling densities and population trends in native species (Koenig 2003). Predicting and quantifying the impact of introduced species on native populations remains a major challenge (Parker et al. 1999, Koenig 2003).

Substantial overlap in foraging niches between the invasive collared-doves and the native mourning dove suggest that interspecific competition for food resources may have a negative impact on the native species (Romagosa 2002, Hayslette 2006). Seed preference experiments indicate that Eurasian collared-doves consume all of the seeds readily taken by mourning doves in addition to whole corn kernels that are not often consumed by the native doves due to morphological limitations (Hayslette 2006, Poling and Hayslette 2006). Thus, the larger size of collared-doves allows them to exploit additional resources and may give them a competitive advantage over the smaller native species.

Despite the potential for interference competition, we failed to find convincing evidence of negative within-site impacts of collared-doves on native dove counts in winter in Florida. In fact, positive within-site relationships between collared-dove counts and numbers of the other dove species were indicated by 13 of the 14 best models in our community analyses. These models also demonstrated that the positive within-site relationship was not merely a reflection of similar habitat preferences among species. The presence of super-abundant food resources at these sites may be masking the negative effects of competition over resources between the invasive and established species. It should be noted, however, that mourning dove, common ground-dove, and rock pigeon all declined in abundance during the sampling period. The only dove species to show an increasing trend in addition to the collared-dove was the white-winged dove. Although native to North America, the white-winged dove was not historically found in Florida and is currently invading the study area.

Our findings may not extrapolate to other parts of North America that are now being colonized by collared-doves because environmental conditions may alter dynamics between species. For instance, resource-based competition may arise in northern environments with greater seasonality and fluctuations in food availability. Negative interactions may also develop if collared-doves reach greater population densities. The results of the current study are only relevant in sub-tropical Florida at the relatively low densities of collared-dove populations. Further, negative interactions need not be in the form of competition for resources. Invasive species may serve as alternate hosts for diseases and parasites, possibly leading to greater rates of infection in populations of native species (Conti and Forrester 1981, Rushton et al. 2006). Eurasian collared-doves in Florida share parasitic helminthes with mourning doves and other species, and can carry paramyxovirus and *Trichomonas gallinae* infections that can cause mortality in native species (Bean et al. 2005). To our knowledge, disease transmission among native and non-native doves has not been studied.

Future directions

The colonization of both Europe and North America by Eurasian collared-doves presents opportunities for comparative analysis of the dynamics and implications of these invasions (Hengeveld 1993). The anisotropic range expansion of collared-doves in North America is also similar to what has previously been described in Europe, suggesting a potential genetic component to the direction of dispersal. The colonization of Europe proceeded most rapidly along a southeast–northwest axis with regions to the north and east being colonized at a slower rate (Kasparek 1996). Several decades following the initial range expansion into Europe, the doves continue to expand into previously unoccupied areas and to increase their population size some areas (Eraud et al. 2007). Similar processes are currently underway in North America.

In-depth study of behavioral interactions between collared-doves and other dove species is also warranted (Kasparek 1996, Romagosa 2002). Questions persist regarding the nature of dominance hierarchies, interference competition, and the potential evolutionary influence of the collared-dove invasion on native species. This colonization event presents a rare opportunity to document behavioral interactions and demographic processes resulting from the rapid expansion of a novel bird species in North America.

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